

Relationships between size, mantle area and zooxanthellae numbers in five species of giant clam (Tridacnidae)

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ABSTRACT: Relationships between body size and both projected mantle area and numbers of symbiotic zooxanthellae were calculated for 5 species of giant clam from the Great Barrier Reef. Parameters were closely correlated in all species, but the allometry of the relationships differed markedly between clam species. Mantle areas were consistently lowest in *Tridacna derasa*. *T. crocea* and *Hippopus hippopus* had the largest mantles at small body size (2 cm), but because of slow length-related increments were soon overtaken by *T. gigas* and *T. squamosa*, the latter developing a mantle area double that of other species at 30 cm length. Similar allometric variations were evident in zooxanthellae numbers. At small size these were much lower in *T. squamosa* and *T. gigas* than in *H. hippopus*, *T. crocea* or especially *T. derasa*; but by 30 cm length *T. squamosa* and *T. gigas* had the largest zooxanthellae populations. When expressed per unit body mass zooxanthellae numbers declined rapidly with size in all species. The rate of decline was most marked in *T. crocea*, this being a function of its rapid length-related increment in flesh mass. This is probably the main factor restricting *T. crocea* to small terminal body size. By contrast, rapid length-related increments in mantle area and zooxanthellae numbers in both *T. gigas* and *T. squamosa* appear to favour the large body size and rapid growth observed in these species. The reason why *T. squamosa* is unable to realize the rapid growth and enormous terminal size observed in *T. gigas* is obscure, but may be a function of the relative reproductive output of these species, which remains unquantified.

KEY WORDS: Giant clam · *Tridacna* · *Hippopus* · Symbiosis · Zooxanthellae

INTRODUCTION

Giant clams of the family Tridacnidae are familiar and conspicuous residents of shallow coral reefs throughout much of the tropical Indo-Pacific. Their most characteristic feature is the enlarged, upwardly directed and usually brightly coloured mantle, which is packed with symbiotic dinoflagellate zooxanthellae. An estimated 95% of the carbon fixed by these algal symbionts is translocated to the host (Fitt 1993, Klumpp & Griffiths 1994), where it normally provides sufficient energy to cover at least the immediate metabolic needs of the hosts (Tench et al. 1981, Fisher et al. 1985, Mingoia 1988, Klumpp & Griffiths 1994, Klumpp & Lucas

1994). Giant clams are also able to filter food particles from the water column (Yonge 1936), although the nutritional significance of this has only recently been quantified. Fitt et al. (1986) first quantified ingestion and digestion of C¹⁴-labelled phytoplankton cells by *Tridacna gigas*, while Klumpp et al. (1992) showed that particulate food constituted 65% of carbon needs in small (0.1 g dry tissue) *T. gigas*, declining to 34% in individuals of 10 g weight. This capacity to exploit both heterotrophic and autotrophic sources of nutrition, plus an ability to divert an unusually high proportion of energy into growth (Klumpp et al. 1992), are no doubt factors that have allowed *T. gigas* to become the largest (137 cm, >500 kg) and fastest growing (>100 mm yr⁻¹) bivalve ever to have existed.

Not all tridacnid clams, however, attain these impressive dimensions—indeed the 9 described species

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differ greatly in both growth rate and terminal size, as well as in the range of coral reef habitats they colonize (Lucas 1988). Thus, *Tridacna gigas* attains a weight an order of magnitude heavier than that of any other species, while *T. crocea* is by far the smallest form, reaching a shell length of only 15 cm. Habitat preferences also vary from the intensely lit waters of intertidal reef flats (*Hippopus hippopus*, *T. crocea*) to depths as great as 33 m in the recently discovered *T. tevoroa* (Ledua et al. 1993).

Two recent studies have attempted to compare the rates of energy acquisition in the various species of giant clam and to correlate these with their habitat preferences and growth performance. Klumpp & Lucas (1994) showed that *Tridacna tevoroa* and *T. derasa* from Tonga function identically in shallow water, but that *T. tevoroa* is able to maintain its photosynthetic capacities at lower light intensities, explaining its ability to maintain a positive energy balance in the deeper waters in which most of the remaining population is found (Ledua et al. 1993). Klumpp & Griffiths (1994) used a similar protocol to compare rates of energy acquisition and expenditure in 4 species of giant clam from the Great Barrier Reef. Their results demonstrate that small (0.1 g dry flesh mass) *T. gigas* not only filter feed at more than 10 times the rate of the remaining species, but photosynthetically fix energy at twice the rate shown in *T. crocea*, 4 times that in *T. squamosa* and 20 times that in *H. hippopus* of equivalent weight. These rates, however, converge with increasing clam size, to differ by less than 2-fold by a weight of 100 g dry flesh mass.

To date the mechanisms underlying these marked size-related changes in photosynthetic rate are unknown. In this paper we make a first attempt at investigating the basis for these differences by examining allometric changes in both mantle area and zooxanthellae population size in 5 of the species for which photosynthetic data are available. It is hoped that these data will provide some insight into why giant clams show such different size-related photosynthetic rates, and hence such a wide range of growth rates and terminal sizes.

METHODS

Collection and maintenance of clams. The *Tridacna gigas* used in this study were cultured specimens obtained from the mariculture facility on Orpheus Island (18° 37' S, 146° 30' E) in North Queensland, Australia. *Hippopus hippopus* and *T. crocea* were collected from intertidal fringing reefs at Iris Point and Pioneer Bay, also on Orpheus Island, respectively. *T. squamosa* were taken at depths of 1 to 10 m in the

lagoon and from the reef flat of Davies Reef (18° 50' S, 147° 38' E) on the Great Barrier Reef and *T. derasa* from the nearby Bowl Reef. All clams were transferred to outdoor 2 × 1 m, 0.5 m deep tanks at the Australian Institute of Marine Science. These tanks were roofed with 50% shade cloth and supplied with flow-through natural sea water at 24 to 27°C. Clams were acclimated for a minimum of 3 wk (and in most cases for several months) in these tanks before use in any experiments.

Mantle areas. Two-dimensional projections of mantle surface areas were computed from 35 mm colour slides shot from directly above each clam, using either a standard 35 mm SLR camera, or in the case of smaller clams, a Nikonos-V underwater camera fitted with Nikonos close-up kit and SB 103 flash. In an attempt to standardize degree of mantle expansion, all photographs were taken between 10:00 and 16:00 h on cloudless days. A 30 cm rule was positioned adjacent to each specimen (and at mantle height) to indicate scale. Clams were left for several hours to gape and expand the mantle fully following any disturbance before being photographed. Some supplementary photographs of large (>40 cm) clams, especially *Tridacna gigas*, were also taken on clear sunny days and in water depths not exceeding 12 m at Bowl, Centipede and Davies Reefs using a Nikonos-V with standard 35 mm lens and SB-103 flash. Between 17 and 27 specimens of each species, selected to cover as wide a size range as possible (see Fig. 1), were photographed.

Mantle areas were digitized using a Sonic-8 digitizer and projected areas calculated using the trapezoidal algorithm for calculating areas from an irregular polygon.

Extraction and enumeration of zooxanthellae. The shell valves of clams used for zooxanthellae counts were jammed apart with wooden wedges and the adductor muscles pried free from the shell with a blunt knife. The mantle was then separated from the visceral mass and divided into left and right halves. The right mantle lobe and the visceral mass of each clam were cut into pieces, placed in separate foil dishes and dried to constant weight at 70°C. Total dry mass was calculated from these values and regressed against shell length.

The left half of each mantle was cut into small pieces in a glass bowl, covered with filtered seawater and then homogenized in a kitchen blender. The homogenate was poured through a double layer of cheesecloth, resuspended in 2 further rinses of filtered seawater, then squeezed dry. The resulting suspension of zooxanthellae was made up to a known volume, which varied from 200 to 2000 ml, depending on clam size. A 1 ml subsample from this concentrate was then diluted to 100 ml and the zooxanthellae in 2 ml of this suspen-

sion counted using a model TA11 Coulter Counter with 140 µm aperture tube. Two dilutions were made up from each clam and duplicate counts made from each. Total zooxanthellae numbers were back-calculated from the mean of these 4 counts.

Near the end of the experiment a more sophisticated Coulter Multisizer became available. This could resolve 256 size channels, relative to the 16 of the TA11 and allowed for a much clearer resolution of the size-frequency peak representing the zooxanthellae. Samples from the last 10 clams were thus counted on both machines. The Multisizer counts so obtained were consistently 30% higher than those from the TA11. As a result all earlier counts made with the TA11 were corrected by a factor of 1.3.

Zooxanthellae counts were not undertaken for *Tridacna gigas*, since measurements derived from the same clam population and using exactly the same extraction technique adopted here are available in Fitt et al. (1993).

Chlorophyll analysis. In order to determine whether zooxanthellae from the various clam species contained different amounts of chlorophyll, subsamples of 10 ml zooxanthellae-concentrate from each clam were analysed for chlorophyll. Samples were filtered onto GF/C filter papers, which were then wrapped in foil and frozen in the dark for later analysis. Filters were subsequently homogenized in 90% acetone, transferred to a 10 ml centrifuge tube for 2 h in total darkness, then centrifuged for 10 min at 3500 rpm. The absorbance of the supernatant was read at 630 and 663 nm and chlorophyll concentrations calculated according to the equations of Jeffrey & Humphrey (1975).

No chlorophyll readings were taken for *Tridacna gigas* since measurements taken using similar techniques and based on the same population of clams are available in Belda et al. (1993).

Statistical methods. All statistics were carried out using the PC version of SAS version 6, with the exception of multiple comparisons after analyses of covariance (ANCOVA), which were done manually, following Zar (1984).

Regression analyses were undertaken using the procedure 'REG' (one of several options for regression analysis in SAS), after appropriate transformations of the data had been carried out. ANCOVAs were done using the procedure for general linear models (GLM). Where the ANCOVA showed that slopes differed between species, no further analyses were done to determine differences between the means, but multiple comparison tests were carried out to determine pairwise differences between the slopes.

The differences in chlorophyll concentration per cell were tested between species using an ANOVA in the GLM procedure of SAS. The subsequent multiple comparison was done with the Ryan-Einot-Gabriel-Welsch multiple range test (SAS 1985).

RESULTS

Mantle areas

Projected mantle areas were closely correlated ($r^2 > 0.91$) with shell length in all 5 of the clam species tested (Table 1, Fig. 1). Intercepts or a values (i.e. mantle areas at 1 cm length) differed significantly between species, ranging from a minimum of only 0.08 cm² in *Tridacna derasa* to 0.31 cm² in *T. crocea*. Slopes of the regression lines fell within the fairly narrow range 2.07 to 2.57, with the slowest length-related increments in mantle area occurring in *T. crocea* and the fastest in *T. squamosa*.

All pairwise comparisons of slopes were significantly different except *Hippopus hippopus* against both *Tridacna crocea* and *T. derasa*.

Calculated mantle areas for clams of each species at standard lengths of 2, 10 and 30 cm are also shown in Table 1. The most noticeable feature of these results is the consistently small mantle area exhibited by *Tridacna derasa*. This is particularly evident in the larger size classes: mantle area at 30 cm shell length being only 18 to 47% of those of other species.

Relative trends in mantle area amongst the remaining species vary markedly with clam size. At small size *Tridacna crocea* has by far the largest mantle, followed by *Hippopus hippopus*. However, because of the relatively small length-related increments (b values) shown by both these species, they are soon overtaken by *T. squamosa* and subsequently *T. gigas*. Thus, by 30 cm length *H. hippopus* has a mantle area smaller than any other species except *T. derasa*. *T. squamosa* and *T. gigas* show the reverse trend, starting life with

Table 1. Regression equations ($MA = aL^b$) relating shell length (L, cm) to projected mantle area (MA, cm²) in 5 species of giant clam. Also shown are the calculated mantle areas for clams of 2, 10 and 30 cm length (30 cm not attained by *Tridacna crocea*, hence parentheses around this value)

Species	a	b	r^2	n	Area at length (cm)		
					2	10	30
<i>Hippopus hippopus</i>	0.211	2.139	0.91	24	0.93	29.1	304
<i>Tridacna crocea</i>	0.305	2.071	0.93	33	1.28	35.9	(349)
<i>T. derasa</i>	0.0765	2.218	0.92	17	0.36	12.6	144
<i>T. gigas</i>	0.109	2.393	0.96	27	0.57	26.9	373
<i>T. squamosa</i>	0.130	2.569	0.97	21	0.77	48.2	810

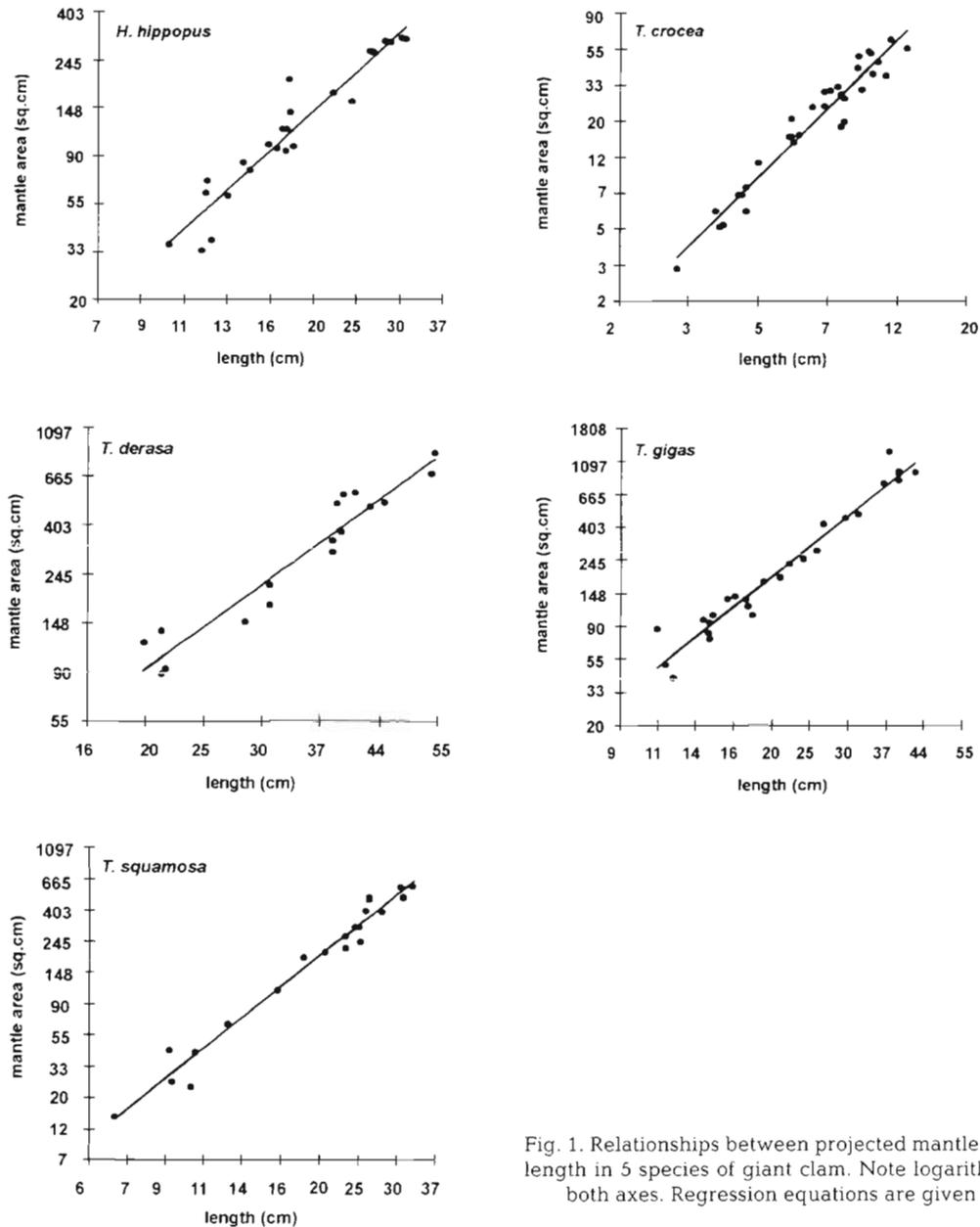


Fig. 1. Relationships between projected mantle area and shell length in 5 species of giant clam. Note logarithmic scales on both axes. Regression equations are given in Table 1

relatively small mantle areas, but expanding these rapidly with size. This trend is particularly marked in *T. squamosa*, which is ranked 4th of the 5 species in terms of mantle area at 2 cm length, but by 30 cm length has a mantle more than twice as large as those of any other species.

Numbers of zooxanthellae per clam

All species show a logarithmic increase in the absolute numbers of zooxanthellae per clam with increasing shell length (Fig. 2). Slopes and intercepts of the

regression equations obtained, as well as calculated numbers of zooxanthellae present in clams of 2, 10 and 30 cm standard length, are shown in Table 2. The intercept or *a* values (zooxanthellae in clams of unit length) varied from a low of 0.5×10^6 cells in *Tridacna squamosa* to a maximum of 16.3×10^6 in *T. derasa* (despite the fact that this species has the smallest mantle area). The slopes, or *b* values, which indicate rate of increase with shell length, varied from 1.54 to 2.76 but show the reverse sequence, the lowest value now occurring in *T. derasa* and the highest in *T. squamosa*. Slopes differed significantly except between *T. crocea* and *T. derasa*.

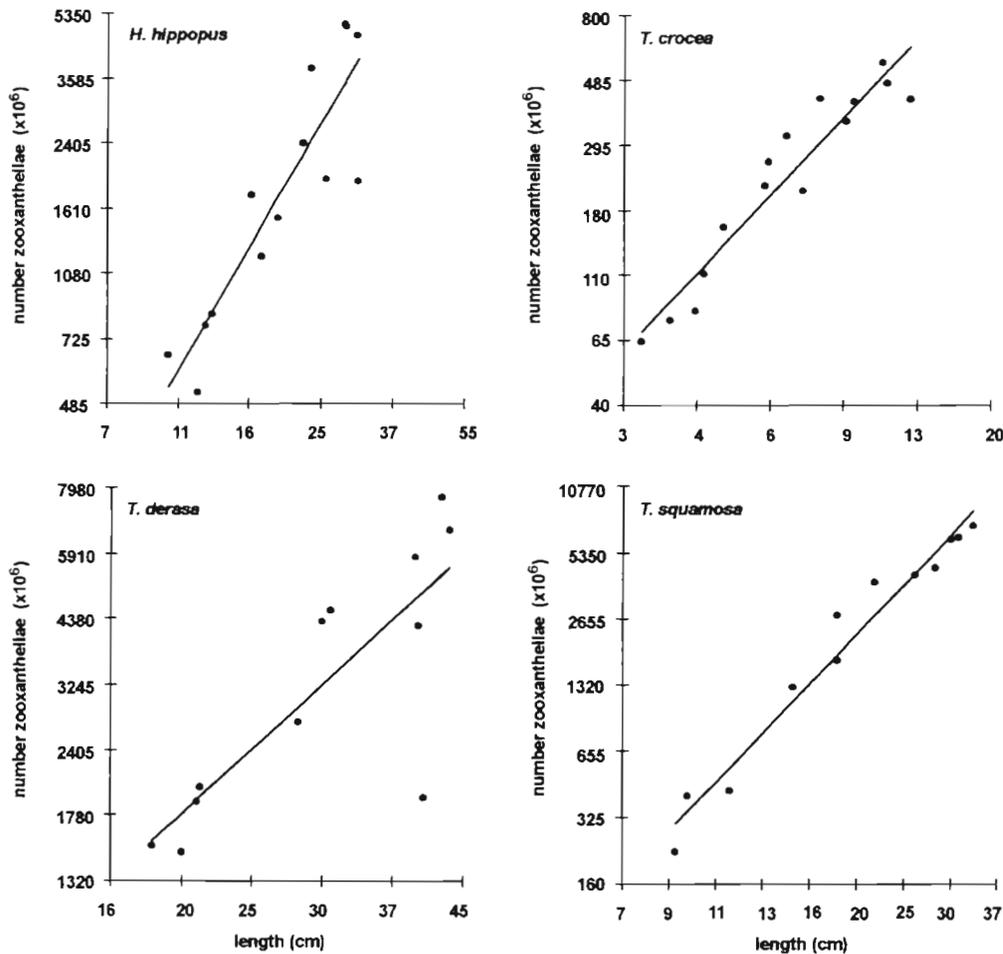


Fig. 2. Relationships between total numbers of zooxanthellae per clam and shell length in 4 species of giant clam. Note logarithmic scales on both axes. Regression equations for these species and *Tridacna gigas* (derived from Fitt et al. 1993) are given in Table 2

The net result is for marked size-related differences in the relative numbers of zooxanthellae between the various species. At a size of 2 cm, for example, the numbers of zooxanthellae per clam differ by more than 10-fold, from a maximum of 47×10^6 in *Tridacna derasa*, through 22×10^6 in *T. crocea*, 17×10^6 in *Hippopus hippopus* and 4.7×10^6 in *T. gigas* to a minimum of 3.4×10^6 in *T. squamosa*. However, this order has almost completely reversed by the time a size of 30 cm is reached, at which point *T. squamosa* has the largest zooxanthellae population (5968×10^6 cells), followed by *T. gigas*, *H. hippopus* and then *T. derasa* at 3068×10^6 (*T. crocea* does not attain this size, although projected values indicate an even lower number of zooxanthellae).

Numbers of zooxanthellae per gram dry body mass were greatest in the smallest

clams of all species tested and decreased steadily with increasing clam size (Table 3, Fig. 3). The numbers of zooxanthellae present in clams of 1 g dry mass (a val-

Table 2. Regression equations ($N = aL^b$) relating shell length (L, cm) and total numbers of zooxanthellae ($N \times 10^6$) in 5 giant clam species. Also shown are calculated zooxanthellae populations in clams of 2, 10 and 30 cm shell length. Data for *Tridacna gigas* adapted from Fitt et al. (1993) (note that x and y parameters were accidentally reversed in the equation as presented in that paper). *T. crocea* does not attain 30 cm, hence this projected value is given in parentheses

Species	a	b	r ²	n	10 ⁶ zooxanthellae at length (cm)		
					2	10	30
<i>Hippopus hippopus</i>	4.2	2.00	0.79	14	16.8	420	3780
<i>Tridacna crocea</i>	6.7	1.73	0.89	15	22.4	362	(2421)
<i>T. derasa</i>	16.3	1.54	0.62	12	47.4	565	3068
<i>T. gigas</i>	0.81	2.54	0.96	22	4.7	282	4592
<i>T. squamosa</i>	0.50	2.76	0.96	12	3.4	288	5968

Table 3. Regression equations ($N = aM^b$) relating number of zooxanthellae ($N \times 10^6$) per gram dry flesh mass (gdm) to dry flesh mass (M, g) in 5 species of giant clam. Data for *Tridacna gigas* are calculated from the regression equation relating length to zooxanthellae numbers given by Fitt et al. (1993) and the length to dry tissue mass relationship in Klumpp & Griffiths (1994). Also shown are calculated densities of zooxanthellae gdm^{-1} for clams of 1, 10 and 100 g dry flesh mass. *T. crocea* does not attain 100 g, hence this value is given in parentheses

Species	a	b	r ²	n	Zooxanth. per gdm at dry mass of		
					1 g	10 g	100 g
<i>Hippopus hippopus</i>	337.6	-0.471	0.77	14	338	114	39
<i>Tridacna crocea</i>	334.3	-0.872	0.92	15	334	45	(6)
<i>T. derasa</i>	347.2	-0.477	0.55	12	347	115	38
<i>T. gigas</i>	177.8	-0.244	-	-	178	101	58
<i>T. squamosa</i>	232.1	-0.309	0.74	12	232	113	56

ues in Table 3) were similar between species, except for *Tridacna squamosa* and *T. gigas*, which had between $\frac{2}{3}$ and $\frac{1}{2}$ the numbers in the remaining species. Slopes of the regression lines (*b* values in Table 3) showed a considerable range, with *T. crocea* exhibiting a much more pronounced size-related decline in zooxanthellae density than any other species. Of the remaining species, *T. derasa* and *H. hippopus* showed very similar trends, while *T. squamosa* and especially *T. gigas* had the slowest rates of decline in zooxanthellae density with increasing body weight.

These trends are clearly illustrated in the calculated zooxanthellae densities in clams of standard mass (Table 3). At 1 g mass, *Tridacna gigas* has by far the lowest cell density at 178×10^6 cells g^{-1} , followed by *T. squamosa* at 232×10^6 cells g^{-1} . The remaining species show values of 330 to 350×10^6 cells g^{-1} . By 10 g mass, *T. crocea* has less than half the density of zooxanthellae (45×10^6) of any other species. At 100 g, *T. derasa* and *Hippopus hippopus* have very similar zooxanthellae populations of 38 to 39×10^6 g^{-1} , considerably less than the 56 and 58×10^6 cells g^{-1} found in *T. squamosa* and *T. gigas*, respectively.

Chlorophyll values

Concentrations of chlorophyll, expressed as μg chl *a* and *c*₂ (the 2 dominant forms of chlorophyll in zooxanthellae; Jeffrey & Humphrey 1975) per 10^6 zooxanthellae varied from a maximum of $6.25 (\pm 1.3 \text{ SD}, n = 12)$ in *Tridacna crocea* through $4.7 (\pm 2.4, n = 10)$ in *Hippopus hippopus* and $4.6 (\pm 0.9, n = 10)$ in *T. squamosa* to a minimum of $4.1 (\pm 1.4, n = 9)$ in *T. derasa*. No size-related trends in chlorophyll concentration per zooxanthella could be detected.

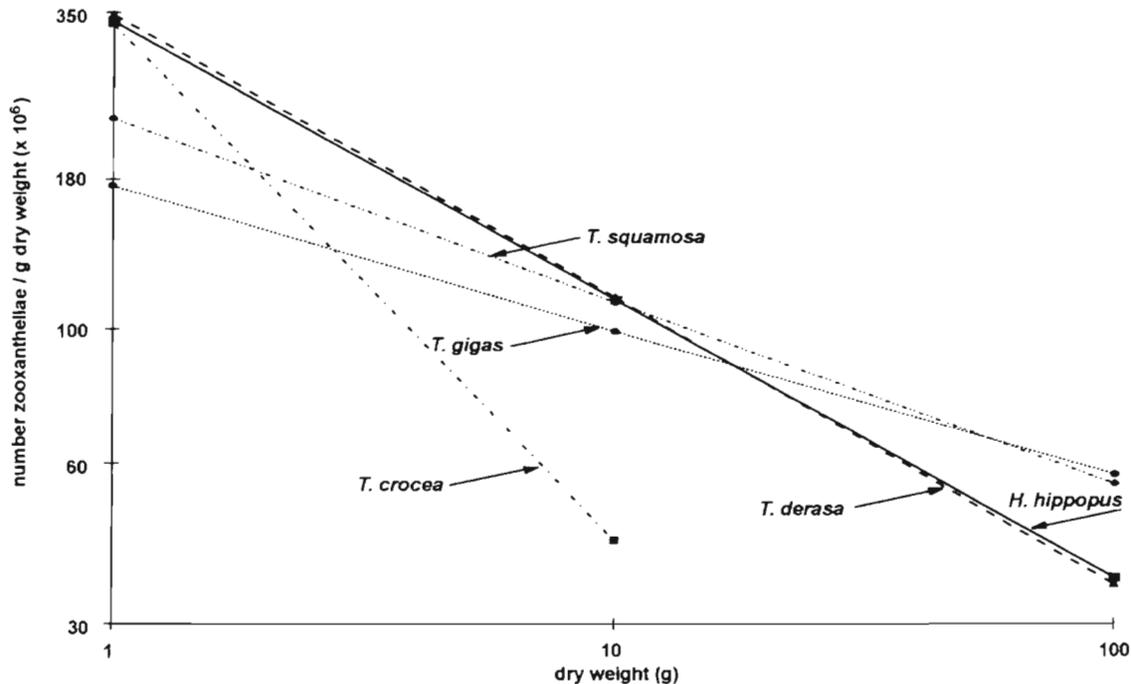


Fig. 3. Relationships between numbers of zooxanthellae per gram dry flesh weight and dry flesh weight in 5 species of giant clam. Note logarithmic scales on both axes. Numbers of zooxanthellae were calculated from the equations in Table 2 and length to dry flesh weight relationships from Klumpp & Griffiths (1994), or in the case of *Tridacna derasa*, our own published data

DISCUSSION

Mantle areas

All the clams studied showed a relative increase in projected mantle area per unit shell length as they increased in size (i.e. exponents of the regression equations exceed 2—the value indicative of an isometric length to area relationship). In practice, this is evidenced by a relative increase in shell breadth and of mantle width with increasing size. The mantle may also become more convoluted in larger specimens. Such 3-dimensional changes in mantle morphology may influence photosynthetic efficiency, but this factor was not considered here.

Of particular significance is the very rapid rate of increase in relative mantle area in *Tridacna squamosa*. The enlarged scutes on the shell of this species may assist in supporting the lateral projections of its mantle, which at large size may cover twice the area of that in any other species. *T. crocea* is also notable in that it exhibits the reverse trend, having a relatively large mantle early in life, but a low *b* value close to 2, so that the mantle area barely keeps pace with increasing shell length at larger sizes. *T. derasa* is also remarkable in its consistently low mantle area throughout life.

Number of zooxanthellae

As would be expected, our results show logarithmic increases in total zooxanthellae numbers with increasing clam length in all species studied. The equations relating zooxanthellae numbers to shell length in *Hippopus hippopus*, *Tridacna crocea* and *T. derasa* all have exponent values lower than those relating mantle area to length (Tables 1 & 2). This indicates a decline in zooxanthellae density per unit mantle area in larger clams. *T. squamosa* and *T. gigas* show the reverse trend and hence have greater densities of zooxanthellae per unit mantle area at larger size. The results of these differing trends are best seen in the figures for total zooxanthellae numbers. These clearly distinguish 2 groups of species: one (*H. hippopus*, *T. crocea* and *T. derasa*) with relatively high zooxanthellae populations early in life and relatively low ones at larger size, and the other (*T. gigas* and *T. squamosa*) which initially harbours far fewer symbionts, but ultimately develops the largest populations.

Calculations of zooxanthellae numbers per gram flesh mass (Table 3) show that such densities decline with increasing clam size in all species sampled. This is to be expected, since the zooxanthellae are almost all confined to the surface layers of the mantle, which, relative to the body as a whole, is essentially 2-dimen-

sional. Clam weight is, however, related to volume, so is a cubic function with a length exponent between 3.2 and 3.5 (see Klumpp & Griffiths 1994). While such relationships are valid for clams >1 cm in length, it should be noted that the symbiotic relationship between clams and their zooxanthellae only commences after metamorphosis—the juveniles acquiring their zooxanthellae through filter-feeding activities (Lucas 1994). Densities of zooxanthellae would hence be low in newly metamorphosed juveniles, as has been shown in *Tridacna gigas* by Fitt et al. (1993).

Absolute zooxanthellae densities per gram flesh mass were fairly consistent between species at small size (Table 3), but declined much more rapidly in *Tridacna crocea* than in the remaining species. Those species with low initial values (*T. gigas*, *T. squamosa*) again achieve the highest densities of symbionts by a weight of 100 g.

Chlorophyll concentrations

Measurements of chlorophyll content per 10⁶ zooxanthellae indicate little interspecific variation in chlorophyll content, other than an elevated value for *Tridacna crocea*. Chlorophyll concentrations obtained here are somewhat higher than those reported for *T. gigas* by Belda et al. (1993), who give values of between about 1 and 3 pg zooxanthella⁻¹ (= µg zooxanthellae 10⁻⁶). Their measurements were, however, expressed as chl *a* content only, whereas we estimated both chl *a* and *c*₂. Chl *c*₂ comprises approximately 30% of total chlorophyll and when this is taken into account there is close correlation between the 2 data sets. Any differences might in any event not represent consistent interspecific patterns, but could be the result of environmental conditions, since it has been established that chlorophyll content per zooxanthella is sensitive to factors such as the nutrient regime (Belda et al. 1993).

Implications for nutrition and growth

Of the parameters measured here one might expect numbers of zooxanthellae per gram of clam tissue weight (Fig. 3) to give the best indication of the relative contribution of phototrophic production to host requirements. These data clearly show a rapid decline in weight-specific zooxanthellae density with size in *Tridacna crocea*. This is a direct result of the rapidly increasing mass at length in this species (for length/weight relationships see Klumpp & Griffiths 1994, Klumpp & Lucas 1994). This results in *T. crocea* having a flesh weight of more than 3× that of any other species by the time it attains 100 mm shell length. Weight-specific variations in zooxanthellae

numbers are less marked amongst the remaining species, although *T. squamosa* and *T. gigas* do have considerably more zooxanthellae g^{-1} than *T. derasa* or *Hippopus hippopus* at larger sizes.

Of course, zooxanthellae number is not the sole variable determining photosynthetic production, which may also be influenced by such factors as location of the zooxanthellae within the tissues, mantle area and clam posture, etc., as well as environmental factors such as water depth, shading, etc. Indeed, direct measurements of photosynthetic rate made by Klumpp & Griffiths (1994) indicate that *Tridacna crocea* is able to maintain a photosynthetic rate comparable with other species, and exceeding that in *Hippopus hippopus*, up to a weight of 10 g. There is, however, a progressive decline in performance with size, so that if *T. crocea* were to attain 100 g, its photosynthetic rate would have declined to about half that of other clam species (Klumpp & Griffiths 1994; their Table 4). The reason why *T. crocea* is able to maintain a better than expected photosynthetic rate, relative to species with more zooxanthellae, could be a function of its higher chlorophyll content per zooxanthella, relatively large mantle area (Table 1), or of the placement of zooxanthellae within the mantle for optimal illumination.

Of the remaining species, *Tridacna gigas* and *T. squamosa* start with relatively low zooxanthellae densities, but because of low weight-specific rates of decline, have the highest densities at sizes over 10 g flesh mass. This is reflected in their high relative photosynthetic rates (Klumpp & Griffiths 1994; their Table 4). *T. derasa* and *Hippopus hippopus* appear to have relatively low weight-specific zooxanthellae populations at large size and indeed have correspondingly low absolute photosynthetic rates (Klumpp & Griffiths 1994, Klumpp & Lucas 1994). Surprisingly, however, both species rank amongst the faster-growing of tridacnids. In the case of *H. hippopus* this can largely be attributed to a very low rate of respiration and an unusually high rate of absorption of ingested food (Klumpp & Griffiths 1994). However, in *T. derasa* both the photosynthetic rate and CZAR (contribution of zooxanthellae to animal respiration) values are low (Klumpp & Lucas 1994), as indeed is the clearance rate.

The above interspecific comparisons are based on clams that were either reared in culture, or transferred to standard laboratory conditions from diverse natural habitats weeks or months prior to experimentation (the exception being the few mantle areas taken from very large individuals in the field). It is recognised that in nature clams may adjust their mantle area, number of zooxanthellae, or chlorophyll concentration per zooxanthella (see above) in response to ambient conditions, confounding any analysis. However, based on our laboratory-conditioned animals it would appear

that the small size attained by *Tridacna crocea* can be associated with a rapid decline in zooxanthellae numbers relative to body weight in that species, which in turn is paralleled by a rapidly declining weight-specific photosynthetic rate (Klumpp & Griffiths 1994). The boring habits of this species may also place a constraint on the terminal size that can be attained. The exceptionally rapid growth rate and large size attained by *T. gigas* may partly be a function of a low weight-specific decline in zooxanthellae density (which becomes particularly significant at very large body size). At small size, however, growth appears to be maintained by an exceptionally rapid rate of filter feeding (Klumpp & Griffiths 1994, their Table 5). All indications suggest that *T. squamosa* has high concentrations of zooxanthellae and fast photosynthetic rates at large size, yet this species shows a relatively poor growth performance relative to *T. gigas* (Klumpp & Griffiths 1994). The reasons for this are obscure, but could include earlier maturity and higher reproductive output than occurs in *T. gigas*. The comparative measures of reproductive output in clam species that are required to make such calculations are not available and remain a promising area for future investigation.

Acknowledgements. We are indebted to David McKinnon and Sheryl Fitzpatrick of AIMS for their assistance with experimental procedures, to David Yellowlees for demonstrating his procedure for the extraction of zooxanthellae and to Kim Navin for use of his digitizer. David Glassom of UCT assisted with the statistical analyses. C.L.G. is grateful to the University of Cape Town for granting him sabbatical leave in order to undertake this study and to the Foundation for Research Development and Vera Davie Study and Travel Bursary Fund for financial support during his visit to Australia. This is AIMS Contribution No. 808.

LITERATURE CITED

- Belda CA, Lucas JS, Yellowlees D (1993) Nutrient limitation in the giant clam—zooxanthellae symbiosis: effects of nutrient supplements on growth of the symbiotic partners. *Mar Biol* 177:655–664
- Fisher CR, Fitt WK, Trench RK (1985) Photosynthesis and respiration in *Tridacna gigas* as a function of irradiance and size. *Biol Bull* 169:230–245
- Fitt WK (1993) Nutrition of giant clams. In: Fitt WK (ed) *Biology and mariculture of giant clams*. ACIAR Proceedings No. 47. Australian Centre for International Agricultural Research, Canberra, p 31–40
- Fitt WK, Fisher CR, Trench RK (1986) Contribution of the symbiotic dinoflagellate *Symbiodinium microadriaticum* to the nutrition, growth and survival of larval and juvenile tridacnid clams. *Aquaculture* 55:5–22
- Fitt WK, Rees TAV, Braley RD, Lucas JS, Yellowlees D (1993) Nitrogen flux in giant clams: size-dependency and relationship to zooxanthellae density and clam biomass in the uptake of dissolved inorganic nitrogen. *Mar Biol* 117: 381–386
- Jeffrey SW, Humphrey GF (1975) New spectrophotometric

- equations for determining chlorophylls *a*, *b*, *c*₁ and *c*₂ in higher plants, algae, and natural phytoplankton. *Chem Physiol Pflanzen (BPP)* 167:191–194
- Klumpp DW, Bayne BL, Hawkins AJS (1992) Nutrition of the giant clam *Tridacna gigas* (L.). I. Contribution of filter feeding and photosynthesis to respiration and growth. *J Exp Mar Biol Ecol* 155:105–122
- Klumpp DW, Griffiths CL (1994) Contributions of phototrophic and heterotrophic nutrition to the metabolic and growth requirements of four species of giant clam (Tridacnidae). *Mar Ecol Prog Ser* 115:103–115
- Klumpp DW, Lucas JS (1994) Nutritional ecology of the giant clams *Tridacna tevoroa* and *T. derasa* from Tonga: influence of light on filter-feeding and photosynthesis. *Mar Ecol Prog Ser* 107:147–156
- Ledua E, Manu N, Bradley RD (1993) Distribution habitat and culture of the recently described giant clam *Tridacna tevoroa* in Fiji and Tonga. In: Fitt WK (ed) *Biology and mariculture of giant clams*. ACIAR Proceedings No. 47. Australian Centre for International Agricultural Research, Canberra, p 147–153
- Lucas JS (1988) Giant clams: description, distribution and life history. In: Copland JW, Lucas JS (eds) *Giant clams in Asia and the Pacific*. ACIAR Monograph No. 9, Australian Centre for International Agricultural Research, Canberra, p 21–32
- Lucas JS (1994) The biology, exploitation, and mariculture of giant clams (Tridacnidae). *Rev Fish Sci* 2:181–223
- Mingoa SM (1988) Photoadaptation in juvenile *Tridacna gigas*. In: Copland JW, Lucas JS (eds) *Giant clams in Asia and the Pacific*. ACIAR Monograph No. 9, Australian Centre for International Agricultural Research, Canberra, p 145–150
- SAS (1985) SAS user's guide: statistics, Version 5 edn. SAS Institute Inc, Cary, NC, p 448–453
- Trench RK, Wethey DS, Porter JW (1981) Observations on the symbiosis with zooxanthellae amongst the Tridacnidae (Mollusca, Bivalvia). *Biol Bull* 161:180–198
- Yonge CM (1936) Mode of life, feeding, digestion and symbiosis with zooxanthellae in the Tridacnidae. *Scient Rep Gt Barrier Reef Exped* 1:283–321
- Zar (1984) *Biostatistical analysis*. Prentice-Hall, New Jersey

This article was submitted to the editor

Manuscript first received: April 3, 1995

Revised version accepted: January 3, 1996